

THE SHELL STRUCTURE OF THE LIASSIC AMMONITE FAMILY DACTYLIOCERATIDAE

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ABSTRACT

Dactylioceratidae are thought to be unique amongst Jurassic and Cretaceous ammonites, in that, as well as the normal main shell with its thin Outer Prismatic, thick Nacreous and thin Inner Prismatic Layers, they also possess an inner shell, consisting of thin Outer Prismatic and thick Inner Nacreous Layers, which is added to the inside of the main shell, but bridges across the inside of the ribs leaving cavities with characteristic flat floors. The inner shell lines the whole of the lateral and ventral parts of the main shell, while its front edge is $\frac{1}{8}$ to $\frac{1}{2}$ whorl behind the mouth border and is similar in shape. It is formed by division of the Inner Prismatic Layer when ventral ribs first develop three whorls after the protoconch. At the rear of the body chamber another new layer, the thick Septal Prismatic Layer, lines the whole of the inside of the shell, including the dorsum, where it bridges across the ribs of the venter of the previous whorl leaving crescent-shaped cavities. Septa are a direct development of that layer, which is present on the dorsum from the mouth of the protoconch, and spreads to line the whole of the shell when the ribs first develop.

The main purpose of the inner shell was probably to smooth the inside of the body chamber to allow easier movement prior to the formation of each septum. The Triassic family Trachyceratidae also possesses an inner shell that is probably similar. The nearest comparable structures in Jurassic and Cretaceous ammonites are dorsal shields, and floors to spines and keels.

I. INTRODUCTION

CLOSE examination of any well-preserved ammonite of the family Dactylioceratidae reveals the presence of two shells on at least the last three whorls up to the adult aperture. The main shell overlies a second inner shell of similar thickness and development. In almost all cases the inner shell does not follow the form of the inner surface of the main shell exactly, but cuts across the inside of the ribs to leave flat-floored rib cavities. The resulting flat tops to the ribs of the inner shell are easily seen without the aid of a hand lens or microscope. When the ammonites are preserved in calcareous nodules, the main shell usually adheres strongly to the outer matrix of the nodule, while the inner shell adheres to the matrix or cast inside the ammonite, so the nodule splits along the junction between the main and inner shells of the ammonite. The outer matrix is then frequently discarded by collectors, and the ammonite that is retained consists of the inner shell only, with characteristic flat-topped ribs.

These features of Dactylioceratidae were first recorded by Buckman (1909 : ix, x), who proposed the terms 'septicosta' and 'septicostate' to describe the hollow ribs cut off by a septum on the inside; he also pointed out that this was a good character by which to distinguish them from homeomorphic Bathonian and later Perisphinctidae which do not have septicostate ribs. No further comment appeared until Guex (1970) described the phenomenon again, and gave photographs and drawings showing the extent of the inner shell in some Bifrons Zone Dactylioceratidae. The macroscopic features of the main and inner shells in species of *Dactylioceras* from the Tenuicostatum Zone in the Upper Lias of Yorkshire were described by Howarth (1973 : 249-252), who included cross-section drawings through the shell structure, and many illustrations in the plates of the different appearances of the inner and outer surfaces of the main and inner shells.

Although the presence of both main and inner shell can be seen in any well-preserved Dactylioceratidae, details of the structures of individual layers have been obscured by recrystallization in all but a few exceptional cases. Thus all the Dactylioceratidae from many different horizons in the Upper Lias of the Yorkshire coast have recrystallized shells in which the original aragonite is not preserved. Only the main features of the main shell and the inner shell as single entities can be seen. They are of interest, however, at horizons where pyrites replacement has occurred, for it is apparent that the main and inner shells behave as independent layers even when they are in close contact, as in the interspaces.* Complete replacement of the inner shell by pyrites sometimes occurs where the attached main shell consists of recrystallized calcite. The junction between the recrystallization and the pyrites replacement corresponds exactly with the junction between the main and inner shells. This independent behaviour of the two shells can only be explained in terms of the layers of which each consists : the thin layer of prismatic crystals (the Inner Prismatic Layer) that occurs between the two must have acted as a barrier to the pyritic replacement that occurred from the inside and prevented it from reaching the main shell.

* The term 'interspace' refers to those parts of the shell between the ribs.

For detailed investigation of the structure of individual layers, specimens have to be used in which the original aragonite is unaltered. Such preservation in British Dactylioceratidae is only found in a restricted area of the Upper Liassic Bifrons Zone clays of western Northamptonshire. Specimens were prepared for examination under a scanning electron microscope (Stereoscan), and all details of the inner shell were revealed. In addition some remarkable dorsal shell layers were discovered, deposited on the venter of the preceding whorl only just in front of the last septum at the rear of the body chamber. These structures partly fill in the spaces between the ribs on the venter of the previous whorl, in a similar fashion to the inner shell which fills in the insides of the same ribs.

II. MATERIAL USED AND PREPARATION

The best material with the original aragonite shell preserved comes from two former brickpits in the *Leda ovum* Beds at Eydon, west Northamptonshire (grid references : SP 535512 and SP 540511). Exposures in the soft clays have long since disappeared, but in the nineteenth century many beautifully preserved specimens of *Peronoceras fibulatum* (J. de C. Sowerby) and *Zugodactylites braunianus* (d'Orbigny) were obtained from the Lower and Middle *Leda ovum* Beds of Fibulatum Subzone, Bifrons Zone age. Most of the specimens consist of fragments of body chambers only, the phragmocone having disappeared, but the final septum and the venter of the previous whorl are preserved in some cases. Two such specimens of *Peronoceras fibulatum* (BM C.67532 and C.77749) provided 23 of the preparations on which this account is based ; both specimens are parts of adult body chambers of about 40–60 mm whorl diameter. Twelve further preparations showing earlier growth stages in septate whorls and immature body chambers of up to 25–30 mm diameter were made from a nodule containing about 50 small specimens (BM C.78546–49 and C.78592–78603) of the same species from the same locality, in which all the whorls are preserved back to the protoconch. Similar aragonite preservation of the same two species occurs in specimens obtained from a former brickpit in the clays of the *Leda ovum* Beds near Badby, Northamptonshire (SP 555586), 8 kilometres (5 miles) NNE of Eydon. An immature example (C.78545) of *Zugodactylites braunianus* from this locality was used to make two preparations of the septate end of the body chamber at about 30 mm diameter.

All the specimens were glued to standard aluminium stubs, then coated with gold prior to examination in the Stereoscan. Pieces of shell taken from various parts of the whorl and mechanically broken to show a clean cross-section were mounted and used without further preparation. Most specimens, however, consist of small portions of shell attached to matrix, cut or broken from the whorls, or whole immature ammonites, which are ground with fine grade silicon carbide, after attachment to the aluminium stub, in order to attain a flat surface or to reach the exact position required in the shell structure. After washing in water, the grinding marks on the surface were removed by etching in dilute hydrochloric acid. In almost all cases application of a 2 per cent solution of HCl for 10–25 seconds was found to be sufficient to remove all traces of grinding from the aragonite part of

the surface. Care had to be taken not to dissolve the aragonite shell to a significantly lower plane than the much harder enclosing matrix or secondary calcite, because this resulted in an uneven aragonite surface and difficulties in gold coating and examination in the Stereoscan. Acetate peels were also made from various parts of some Yorkshire Dactylioceratidae that had been cut in half in the plane of coiling. These were used to check the extent of the main and inner shells and the dorsal shell layers. About 800 Stereoscan photographs were taken altogether, and the small proportion reproduced here are those that illustrate the structures to best advantage.

For reasons that are discussed later (p. 63) the nomenclature used in this paper is as follows :

- | | | |
|---------------------------|---|-------------|
| 1. Outer Prismatic Layer | } | Main shell |
| 2. Nacreous Layer | | |
| 3. Inner Prismatic Layer | | |
| 4. Outer Prismatic Layer | } | Inner shell |
| 5. Inner Nacreous Layer | | |
| 6. Septal Prismatic Layer | | |

Drawings of the complete shell structure of the near-adult ammonite and of the development of the inner shell during ontogeny are given as Text-figs 1 and 2, in order to facilitate the understanding of the complicated structure.

III. THE MAIN SHELL

The main shell in Dactylioceratidae is the same as in all other ammonites : it consists of a thin Outer Prismatic Layer, a thick Nacreous Layer and a thin Inner Prismatic Layer. On the adult body chambers of the specimens examined the thickness of the main shell is about 0.3 mm at the crests of the ribs and about 0.18 mm at the bottom of the interspaces between ribs, at a whorl diameter of about 50 mm. The bulk of this thickness consists of the Nacreous Layer : the thin tablets of aragonite (Pl. 1, fig. 7) are arranged in vertical columns giving the typical appearance at low magnifications of columnar nacre (Pl. 1, figs 1, 5). The Outer Prismatic Layer is usually not well preserved on the exposed parts of the whorls that were surrounded by the enclosing matrix. It is best seen on the venter of the penultimate whorl, where it is revealed as a very thin layer of vertical prisms of aragonite only about 0.0025 mm thick (Pl. 1, fig. 7). The Inner Prismatic Layer (like all other structures on the inside of the shell) is better preserved, for it was not liable to be removed with the matrix. It is generally much thicker than the Outer Prismatic Layer, being 0.01–0.02 mm thick, and the prisms are noticeably longer (Pl. 1, fig. 6). The adoral edge of the Inner Prismatic Layer was not found in any specimen, but it must be close behind the aperture, because its inner surface is covered by the inner shell which is formed $\frac{1}{8}$ to $\frac{1}{4}$ whorl behind the aperture.

The adult aperture of most species of Dactylioceratidae is constricted by a marked thickening on the inside of the shell. The outer surface of the shell is unaffected, but the Nacreous Layer thickens below the last six to eight ribs until it is three or four times the normal thickness under the penultimate rib. A section through

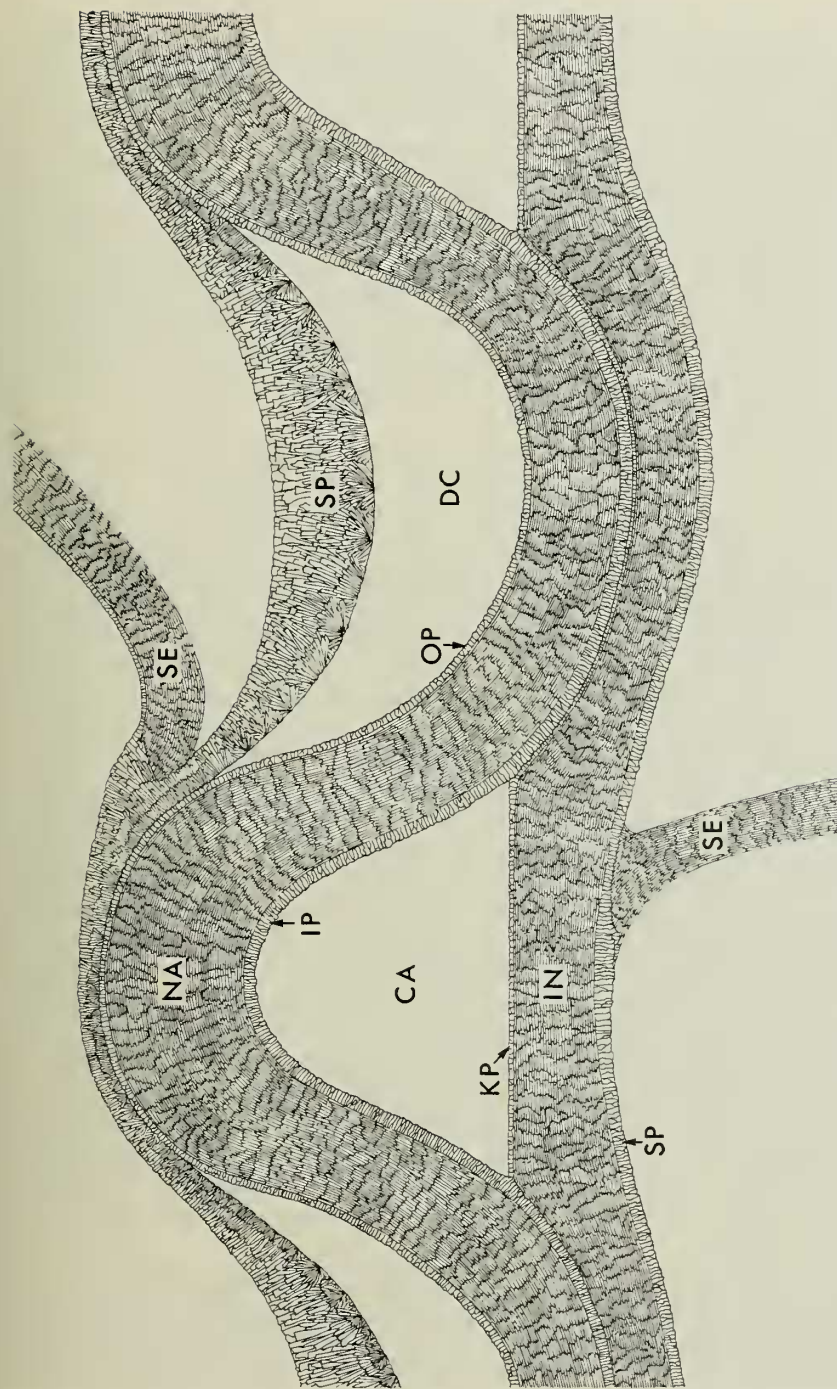


FIG. 1. The full shell structure at the point where the final adult body chamber septum is attached to the middle of the venter of the previous whorl. Shell diameter at final septum c 45 mm; diameter of previous whorl shown here c 28 mm. For abbreviations see p. 67. Drawing based on Pl. 3, fig. 2. The thicknesses of all layers are correct, except for the Inner Prismatic and both Outer Prismatic Layers which are exaggerated for clarity. Note that the Outer Prismatic Layer (KP) of the inner shell is continuous below the middle, but absent above the middle, reflecting the differences observed in specimens. Approx. $\times 125$.

such a constricted aperture was obtained by grinding a Yorkshire coast *Dactylioceras tenuicostatum* (Young & Bird) inside a nodule until the desired position was obtained (Pl. 1, fig. 4). The adoral end of the Inner Prismatic Layer cannot be seen in this fully-grown adult owing to recrystallization. Many specimens show that the constriction affects the whole of the ventral and lateral parts of the aperture. In a few specimens dorsal deposits on top of the venter of the previous whorl can be seen, which correspond in extent with the thickening of the aperture. They sometimes take the form of partitions bridging the spaces between the ribs, as was found in a Yorkshire coast specimen of *Dactylioceras semicelatum* (Simpson) figured in an earlier paper (Howarth 1973 : 251, fig. 4B, partitions P). In this example the dorsal partitions occur only over a short length of the venter of the previous whorl at the adult aperture, and there are none on the dorsum of the rest of the body chamber until the different dorsal deposits of the Septal Prismatic Layer are reached just in front of the final septum.

IV. THE INNER SHELL

The Inner Shell in Dactylioceratidae consists of two layers : a thin Outer Prismatic Layer and a thick Inner Nacreous Layer. The general thickness and development of the layers are similar to those of the main shell, except that the Outer Prismatic Layer has a less well-developed prismatic structure and is not always continuous between the ribs. One of the specimens from Eydon (C.67532) was cut along the middle of the side of the whorl about $\frac{3}{8}$ whorl before the adult aperture, and the precise point of growth of the inner shell was revealed. The front edge of the Outer Prismatic Layer has reached two-thirds of the way across the inside of a rib (Pl. 1, fig. 1) so that the flat floor to this rib cavity is incomplete. This must be the front edge of the inner shell, because the next rib in front has no rib cavity, while the next rib behind has an empty rib cavity floored by a complete partition of the Outer Prismatic Layer of the inner shell (Pl. 1, fig. 5). At higher magnifications this Outer Prismatic Layer is seen to consist of an aragonite sheet with a poorly developed prismatic structure, about 0.0025 mm thick (Pl. 1, fig. 3). The growth of the front edge of the inner shell is not complete on the side of the whorl in this ammonite, so the gradual formation of the Inner Nacreous Layer is seen. The Outer Prismatic Layer occurs alone from its front edge (Pl. 1, figs 1, 3) to just behind the next adapical rib, where the beginning of the Inner Nacreous Layer is seen (Pl. 2, fig. 6) as small plates of aragonite adhering to the inner surface of the Outer Prismatic Layer. Below the next rib adapically the Inner Nacreous Layer has thickened (Pl. 2, fig. 1), and the aragonite plates now being added are as large as those of the Nacreous Layer of the main shell. The layer thickens further and quickly becomes similar in thickness to the Nacreous Layer of the main shell at the same point (Pl. 1, fig. 2).

The junction between the main and inner shells in an interspace on the side of the whorl of C.67532 is illustrated in Pl. 2, fig. 3 ; the obvious parting is between the inner surface of the Inner Prismatic Layer of the main shell and the outer surface of the Outer Prismatic Layer of the inner shell, and the Inner Nacreous Layer is

very thin and only partially developed at this point. The Outer Prismatic Layer of the inner shell is not always continuous, however, for on the venter of C.67532, where the inner shell is much more fully grown, the Outer Prismatic Layer only occurs as flat floors to the rib cavities, and is absent between the ribs. In the corners of the rib cavities in this specimen and in C.77749 (Pl. 2, fig. 5) the end of the Outer Prismatic Layer forming the flat floor abuts against the inner surface of the Inner Prismatic Layer of the main shell, and the Inner Nacreous Layer curves round and comes into contact with the same surface. The Outer Prismatic Layer of the inner shell can always be seen forming the floors to the rib cavities, though, especially when a cavity is empty, there is almost always a layer of secondary calcite crystals on top of the floor (Pl. 2, fig. 2).

V. THE DORSAL SHELL

The dorsal shell, which is the overlap of the main shell on to the venter of the previous whorl, is poorly developed in Dactylioceratidae. It is not clear to what extent the Outer Prismatic Layer of the main shell extends on to the venter of the previous whorl, which would have been covered by the thin chitinous periostracum (black layer of *Nautilus*). In some places there is an apparent remnant of the layer or more often merely a parting, but in other places it seems that the Nacreous Layer of the main shell was laid down directly on the venter of the previous whorl. This part of the Nacreous Layer is thin and wedges out within a quarter of the way across the venter, so that the middle half of the venter of the previous whorl is not covered by dorsal shell. In three specimens examined, the Inner Prismatic Layer of the main shell was found not to be a component of the dorsal shell because in each case it wedged out at the umbilical seam contact. The inner shell also wedges out exactly at the umbilical seam contact, and therefore it does not occur at all in the dorsal shell. Pl. 2, fig. 4 shows the dorsal shell above the venter of the previous whorl and the end of the inner shell above the umbilical seam, and Pl. 2, fig. 7 shows the detail of the contact between dorsal shell and venter of the previous whorl. The absence of the Inner Prismatic Layer is apparent in the latter figure and also in Pl. 3, fig. 1. The dorsal shell is fully in contact with the previous whorl at the umbilical seam contact, but further in it bridges across the tops of the ribs of the previous whorl as soon as they have attained any significant relief, then it quickly wedges out. The dorsal shell is formed at the same time as the rest of the main shell, i.e. near the mouth border, and is probably complete before deposition of the inner shell $\frac{1}{8}$ to $\frac{1}{4}$ whorl behind the aperture. A completely different deposit that covers the whole of the dorsum including the dorsal shell is the Septal Prismatic Layer, formed at the rear of the body chamber.

VI. THE SEPTAL PRISMATIC LAYER

A prismatic layer that is closely connected with the formation of the septa is developed in all whorls after the onset of strong ribs, and also occurs on the dorsum of earlier whorls. In the adult it has been investigated in detail in two of the

Northamptonshire specimens: C.77749 was sectioned longitudinally (in the plane of coiling) through the final septum and the adjacent part of the body chamber; C.78545 was sectioned in the plane of the final septum, then successively further forwards, and finally in a longitudinal plane to reveal the oral end of the layer. The Septal Prismatic Layer is a thick layer of large prismatic crystals which lines the whole of the body chamber. Its point of formation is not more than $\frac{1}{8}$ whorl in front of the final septum, this being a distance roughly equal to the diameter of that septum. On the lateral and ventral parts of the whorl it is attached directly to the inside of the inner Nacreous Layer of the inner shell, with which it maintains intimate contact over the whole surface because of the greatly reduced rib relief of that surface. In septate whorls (Pl. 4, fig. 1) it is a fairly thin layer of parallel prismatic crystals attaining about 0.01 mm in thickness. In adult body chambers the layer is much thicker, attaining 0.05–0.07 mm just in front of the final septum, and thus it may be as thick as the Inner Nacreous Layer to which it is attached. Thus Pl. 4, fig. 2 shows the very thick prismatic layer immediately adjacent to the final septum; the layer steadily diminishes adorally (Pl. 4, fig. 3; Pl. 3, fig. 3) and disappears at its adoral growing edge which is only 12 mm in front of the final septum.

On the dorsum of the whorl the Septal Prismatic Layer takes on a considerably different aspect. It is laid down over the outside of the venter of the previous inner whorl, where the ribs are in full relief, and dorsal shell is absent in the middle of the venter. The layer maintains contact only with the crests of the ribs, and bridges across the spaces between ribs as thick crescent-shaped layers leaving cavities (Text-fig. 1; Pl. 3, fig. 4). The cavities themselves are crescent-shaped, unlike the cavities left inside the ribs by the inner shell which always have flat floors. By bridging across in this way the relief of the ribs on the venter of the previous whorl is reduced to approximately half. The second respect in which the dorsal part of the Septal Prismatic Layer differs from the ventral and lateral parts is that even over the crests of the ribs the prismatic crystals do not grow directly on the outside of the Outer Prismatic Layer of the previous whorl, presumably because of the presence of the chitinous periostracum, which is not now preserved, but is represented by a parting or secondary material. So the prisms of the Septal Prismatic Layer grow from a few centres of crystallization as radiating bunches of small prisms, becoming larger and sub-parallel when adjacent bunches touch and intermingle (Pl. 3, fig. 6). The crescent-shaped parts of the layer between the ribs are much thicker and the radiating bunches giving rise to large prismatic crystals are more marked (Pl. 3, fig. 5). At the edge of the dorsum there is a transition zone between the mid-dorsum part and the side of the whorl part of the Septal Prismatic Layer: here the main shell Nacreous Layer forms the dorsal shell, and the Septal Prismatic Layer is attached directly to its inside surface (Pl. 3, fig. 1).

The septa are a direct development of the Septal Prismatic Layer. At the point of attachment of a septum anywhere around its edge the large prismatic crystals of the Septal Prismatic Layer change almost instantaneously into the nacreous crystals of the septum (Pl. 4, figs 4–6). The septum is not usually added to the

inside of the Septal Prismatic Layer ; rather, it is a continuation of the growth of that layer, which is thickened immediately adoral to the septum by approximately the thickness of the septum. This added thickness diminishes gradually until the point of attachment of the next septum is reached. On the dorsum, however, there is sometimes evidence of discontinuities within the Septal Prismatic Layer, perhaps indicating that it started growth somewhat before the lateral and ventral parts of the layer, and the septum may be added on to the inside. Thus Pl. 4, fig. 6 shows a septum attached to a mid-dorsal part of the Septal Prismatic Layer which is divided by partings into two layers at one side of the confluence and three layers at the other side ; further to the left of the confluence the two layers become equal in thickness. The mid-dorsum in another specimen has a normal single Septal Prismatic Layer, thin over the rib crests (Pl. 5, fig. 1) and much thicker between the ribs (Pl. 5, fig. 4), which is succeeded by a thin smooth layer with a marked 'building-block' structure in some places, and the septum is attached to the inside of the building-block layer (Pl. 5, fig. 1). At the point of attachment the nacre of the septum changes rapidly into a thick mass of prismatic crystals (Pl. 5, fig. 1) which diminishes in thickness adorally (Pl. 5, fig. 4) and disappears before the crest of the next rib (Pl. 5, fig. 5), where the building-block layer alone is attached to the inside of the Septal Prismatic Layer.

Formation of the Septal Prismatic Layer was found to be more irregular on the dorsum of one specimen. In some places the crescent-shaped layers between the ribs are thicker than usual, and they are formed by growth of radiating masses of prisms in the upper half of the layer, as well as the usual growth of prisms from the base (Pl. 6, fig. 1). In almost all cases this leaves cavities, which are sometimes very large, in the middle of the Septal Prismatic Layer (Pl. 5, fig. 2). In another part of the same specimen two Septal Prismatic Layers are formed between the ribs (Pl. 6, fig. 2) : the first layer is almost in contact with the outer surface of the shell, but it is truncated before reaching the tops of the ribs by a second layer which passes over the ribs, and passes from crest to crest of the ribs leaving cavities below like the normal development of the Septal Prismatic Layer. This type of double layer can be explained by a movement of the mantle surface to a higher position between the ribs after it had initiated secretion of the first layer lower down. Occasionally radiating masses of prismatic crystals are formed in the cavity below a Septal Prismatic Layer that is otherwise normally developed (Pl. 6, fig. 3).

Most of the septa that have been examined in these adult or near-adult specimens consist of a single layer of nacreous crystals, but the final adult body chamber septum in *C.77749* (Pl. 3, fig. 2) also has a thin adoral layer of prismatic crystals (Pl. 5, fig. 3).

VII. ONTOGENETIC DEVELOPMENT

The above descriptions of main shell, inner shell, Septal Prismatic Layer and septa were taken from adult or near-adult body chambers of two specimens of *Peronoceras fibulatum* and one of *Zugodactylites braunianus*. Light microscope examination of the shell surface and sectioned specimens of many other species of Dactylioceratidae

suggests that these are constant features that apply to all whorls after the onset of strong ribs. In many Dactylioceratidae that have approximately seven whorls up to the adult mouth border, this refers to the outer $3-3\frac{1}{2}$ whorls from a diameter of approximately 10 mm upwards. Earlier growth stages, from the mouth of the protoconch through the smooth early whorls and up to the formation of the ribs, have a simpler structure, which was investigated with a view to tracing the development of the inner shell. For this purpose twelve immature specimens of *P. fibulatum* were sectioned to reveal the inner whorls, some having body chambers at less than 6 mm maximum whorl diameter. The larger whorls on six of them confirmed that the shell structure after strong ribs are fully developed is the same as in the adult. The description that follows is based on six specimens that were sectioned in the plane of coiling through the centre of the protoconch, and two that were sectioned to expose a spiral surface passing through the middle of the side of the whorl, to show the commencement of ribs on the whorl side.

(a) *Protoconch, first whorl and nepionic constriction*

The shell structure of early growth stages has been described for several different ammonites by Birkelund (1967), Birkelund & Hansen (1968), Erben, Flajs & Siehl (1969) and Drushits & Khiami (1970). All the Dactylioceratidae that have been investigated are similar. The protoconch wall consists of a single layer of sub-prismatic crystals (Pl. 6, fig. 4). Just before the mouth of the protoconch a second similar layer appears on the inside (Pl. 5, fig. 6), and the first layer wedges out close to the protoconch mouth (Pl. 7, figs 2, 3). The second prismatic layer then thickens and forms the wall of the first whorl up to about $\frac{1}{16}$ whorl before the nepionic constriction (Pl. 6, fig. 6). In five different specimens the nepionic constriction occurs $\frac{13}{16}$ whorl after the mouth of the protoconch. About $\frac{1}{16}$ of a whorl earlier a nacreous layer is added to the inside of the prismatic layer, which itself diminishes considerably in thickness (Pl. 6, fig. 5). At the nepionic constriction the prismatic layer is folded back on itself through 180 degrees, a new prismatic layer starts on the inside of the nacreous layer and cuts obliquely across touching the inside of the folded-back part of the old prismatic layer, then reaches the outside of the shell and continues forwards as the Outer Prismatic Layer of the main shell (Pl. 7, fig. 1). The Nacreous Layer of the main shell is added on the inside starting near the commencement of the Outer Prismatic Layer.

(b) *Smooth whorls after the nepionic constriction*

Between the nepionic constriction, $\frac{13}{16}$ whorl after the mouth of the protoconch, and the start of the ribs at $2\frac{1}{4}-2\frac{1}{2}$ whorls on the side of the whorl and $3-3\frac{1}{4}$ whorls on the venter, there are $1\frac{1}{2}-2$ whorls without ornament. At first the Outer Prismatic and the Nacreous Layers are of approximately equal and steadily increasing thickness (Pl. 7, fig. 7). The start of the Inner Prismatic Layer occurs at $1\frac{1}{4}-1\frac{3}{4}$ whorls, where the shell has reached a total thickness of about 0.02 mm (Pl. 7, fig. 8). The Inner Prismatic Layer has noticeably smaller prisms at first than the Outer Prismatic Layer; it increases rapidly in thickness, partly at the expense of the Nacreous

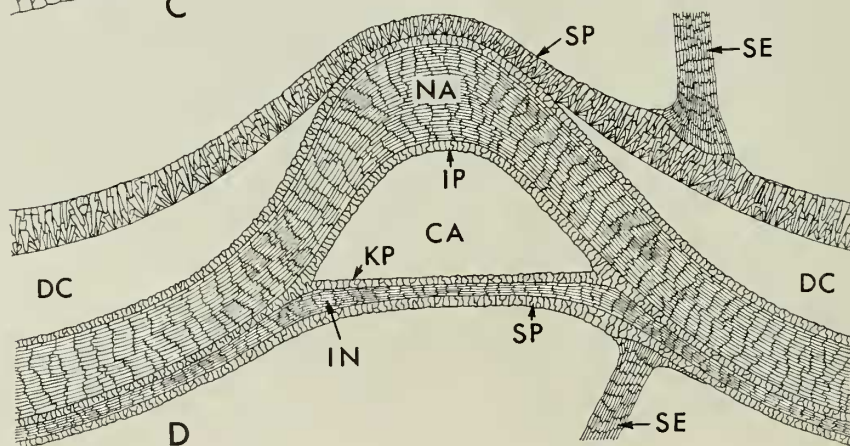
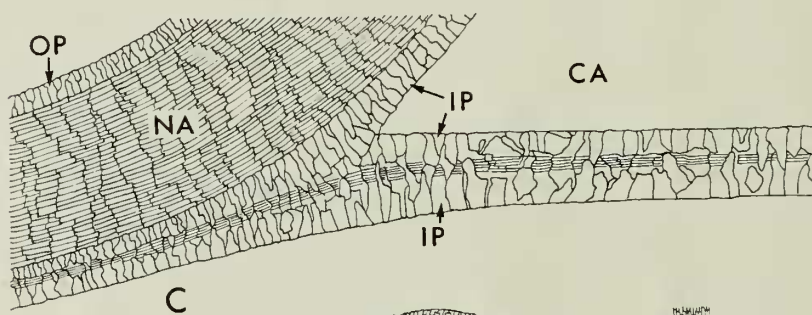
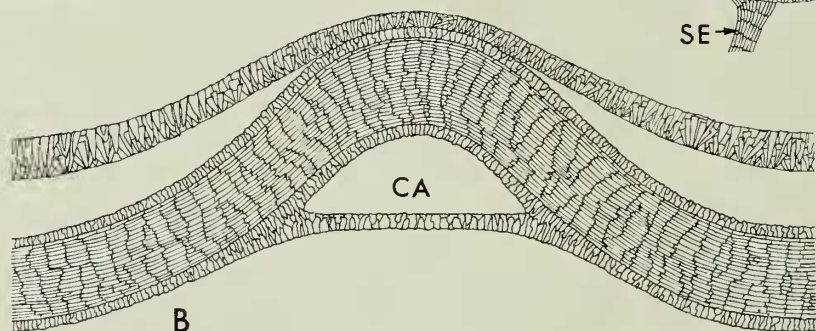
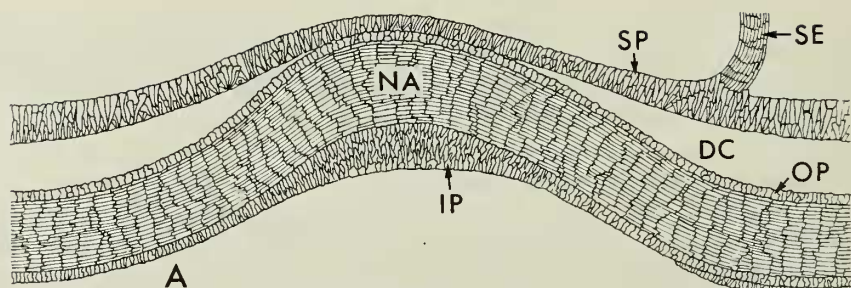
Layer (Pl. 7, fig. 5), and at about 2 whorls it is much thicker than the Outer Prismatic Layer (Pl. 7, fig. 9). The Nacreous Layer then thickens again, so that by the time the ribs commence at $2\frac{1}{4}$ – $3\frac{1}{4}$ whorls it is the thickest of the three layers, and the total shell thickness is about 0.06 mm (Pl. 7, fig. 6).

(c) *Development of the ribs and the inner shell*

Ribs commence on the side of the whorl at $2\frac{1}{4}$ – $2\frac{1}{2}$ whorls and about 3 mm shell diameter. The venter remains smooth for a further $\frac{3}{4}$ whorl, then ventral ribs begin at 3 – $3\frac{1}{4}$ whorls and 5–6 mm shell diameter. The ribs start as low undulations and increase slowly in strength, and a rough assessment is that the ribs on the side of the whorl take 1 – $1\frac{1}{4}$ whorls until the amplitude equals half the crest to mid-trough distance (half the wavelength), while the ribs on the venter attain the same amplitude after about $\frac{3}{4}$ whorl. The shell structure of the previous smooth whorls remains unaltered during most of the development of the ribs on the side of the whorl (Pl. 8, fig. 4). Changes in the structure commence when the ventral ribs begin to develop at about $3\frac{3}{8}$ whorls and 7 mm diameter, and they affect the ribs on both the venter and the side of the whorl equally. First the Inner Prismatic Layer becomes thicker underneath the rib (Pl. 8, fig. 1). After only one to three further ribs the Inner Prismatic Layer splits in the middle (Pl. 8, figs 2, 3); the outer part remains in contact with the Nacreous Layer below the crest of the rib, while the inner part forms a flat floor across the inside of the rib leaving a cavity above. This is the first appearance of cavities inside the ribs, and at this stage the cavities are, in fact, inside the Inner Prismatic Layer. After a further period of growth and increase in size of the ribs, which varies between a few ribs and about $\frac{1}{4}$ whorl, the first signs of a nacreous layer begin to appear in the middle of the Inner Prismatic Layer. This is the start of the Inner Nacreous Layer of the inner shell. In those parts of the shell between the ribs, small flat plates of nacre develop in the middle of the Inner Prismatic Layer (Pl. 8, fig. 5). Similar plates of nacre develop in the middle of the prismatic layer that forms the floor to each rib cavity (Pl. 8, fig. 6). The rib cavity floors are now divided into three parts: the prismatic layer that forms the floor itself and henceforth is called the Outer Prismatic Layer of the inner shell; at these early growth stages it occurs only below rib cavities, but later it occurs between the ribs as well, and is clearly added to the inside of a fully grown Inner Prismatic Layer (Pl. 2, fig. 3). The middle layer is the Inner Nacreous Layer which thickens steadily during further ontogenetic development (Pl. 9, figs 1, 2) until it attains a thickness comparable with its development in the adult (Pl. 9, fig. 4). The third layer is the innermost prismatic layer, which soon becomes closely connected with the attachment of the septa (Pl. 9, fig. 3) and merges with the Septal Prismatic Layer that is already present on the dorsum.

(d) *Insertion of septa and development of the Septal Prismatic Layer*

The prosepium and primary septum are at the mouth of the protoconch and consist of prismatic crystals. The next septum (Pl. 7, fig. 2) and all succeeding septa consist of nacreous crystals. At the point of attachment to the shell wall the



structure of each septum changes rapidly to prismatic crystals. At the dorsal part of the septal attachment (i.e. the attachment to the outside of the venter of the previous whorl) the prismatic crystals form a continuous layer which extends from septum to septum and is called the Septal Prismatic Layer. The lateral and ventral parts of the septal attachment consist of a small 'foot' of prismatic crystals which does not extend far along the inside of the shell wall. However, after the onset of ribs and the formation of the Inner Nacreous Layer, the Septal Prismatic Layer spreads from its original dorsal position to line the whole of the lateral and ventral parts of the inside of the shell, and each septum is now a direct development of that layer all around its periphery (Pl. 4, figs 4-6). Illustrations of the ventral part of the septal attachment are as follows: immediately after the mouth of the protoconch, Pl. 7, fig. 3 (this is the first septum); attachment to the inside of the nacreous layer immediately before the nepionic constriction, Pl. 6, fig. 5; to the inside of the Nacreous Layer after the nepionic constriction but before the Inner Prismatic Layer develops, Pl. 7, fig. 4; to the inside of the Inner Prismatic Layer, Pl. 10, fig. 4; to the inside of the Inner Prismatic Layer during the early stages of rib formation, Pl. 9, fig. 5; and finally, after development of the Inner Nacreous Layer, the septa are in continuity with much of the thickness of the Septal Prismatic Layer, which now lines the inside of the venter (Pl. 8, fig. 7) as well as the lateral and dorsal parts of the whorl. At larger sizes ventral septal attachment has already been shown in Pl. 4, fig. 5.

The Septal Prismatic Layer first appears on the dorsum in the first whorl after the protoconch. It probably occurs continuously from the mouth of the protoconch, but in the material available it is first seen just over one whorl after the protoconch as a continuous thin layer added on top of the previous whorl (Pl. 7, fig. 3). The continuity of the Septal Prismatic Layer is more apparent about a $\frac{1}{2}$ whorl later where another septum is attached (Pl. 6, fig. 6), and it is quite clear at the nepionic constriction (Pl. 7, fig. 1), where it is seen to extend between two septa attached to the outside of the shell and consists of small prismatic crystals. It occurs in this form as a continuous dorsal layer throughout the next few whorls, though it is sometimes missing or detached from the outside of the venter of the previous whorl owing to faulty preservation, such as in Pl. 7, fig. 5. A dorsal septal attachment

FIG. 2. Series illustrating the development of the inner shell, based on C.78594 and C.78598, at shell diameter of c 6.5 mm; for abbreviations see p. 67.

A - Inner Prismatic Layer considerably thickened below rib; septum on inside has foot of prismatic crystals attached to fully formed Inner Prismatic Layer; dorsal Septal Prismatic Layer and a septum in the next outer whorl above the rib. $\times 275$.

B - Two ribs adoral to A; Inner Prismatic Layer now divided and part of it forms the floor below the hollow rib. $\times 275$.

C - Eight ribs adoral to A; first appearance of the nacreous crystals of the Inner Nacreous Layer in the middle of the Inner Prismatic Layer. $\times 750$.

D - About 15 ribs adoral to A; Inner Nacreous Layer now well formed, and ventral part of the Septal Prismatic Layer on the inside shows some continuity with the septum; dorsal Septal Prismatic Layer of the next outer whorl on the outside shows considerable continuity with the septum. $\times 275$.

two whorls after the protoconch is shown in Pl. 10, fig. 5, and another to the shell at the point where ribs first commence is seen in Pl. 9, fig. 5. As soon as the Septal Prismatic Layer is laid down on top of ribs that have attained significant relief, it no longer maintains contact with the outside surface of the shell between the ribs, but bridges across the tops of the ribs leaving slender cavities below (Pl. 10, fig. 1). At this stage the Septal Prismatic Layer consists of longer prisms radiating in bunches from the bottom surface of the layer (Pl. 10, fig. 3), and septa are continuous with the outer part of the layer (Pl. 10, fig. 2). Further development consists of thickening of the Septal Prismatic Layer until it attains the appearance in the adult as already described.

(e) *Position of secretion of individual layers*

The Outer Prismatic Layer and the Nacreous Layer of the main shell are secreted at the mouth border by the front edge of the mantle. In order to maintain strength and rigidity, formation of the Nacreous Layer must proceed very quickly behind the Outer Prismatic Layer; in fact it seems probable that the necessary strength and immunity from injury could only be attained by growth to full thickness in the space of one or two ribs behind the mouth border. The position of formation of the Inner Prismatic Layer changes during ontogeny. In an immature specimen which had a body chamber at a stage before the development of ventral ribs, the Inner Prismatic Layer was formed in the apical half of the body chamber, but sufficiently so far forwards that when the septa were inserted they were added to the inside of a fully formed Inner Prismatic Layer. During development of the ribs and the inner shell, the point of formation of the Inner Prismatic Layer moves further forwards in the body chamber, because it is always in front of the growing edge of the inner shell. During early stages of rib formation the layer is secreted at about the middle of the body chamber, but by the time the adult is reached secretion occurs only $\frac{1}{8}$ whorl behind the mouth border.

When the inner shell was first formed the two constituent layers (the Outer Prismatic Layer and the Inner Nacreous Layer) were secreted $\frac{1}{4}$ – $\frac{3}{8}$ whorl in front of the last septum. As growth proceeded, the position of secretion moved steadily forwards in the body chamber, until it was formed $\frac{1}{8}$ – $\frac{1}{4}$ whorl behind the mouth border in the adult. The formation of the inner shell by division of the original Inner Prismatic Layer left the inner half of that layer on the inside of the body chamber. Observations on three immature specimens suggest that as soon as the Inner Nacreous Layer had grown to a significant thickness (i.e. equal to that of the original Inner Prismatic Layer), then secretion of the prismatic layer on the inside moved quickly back to a position just in front of the final septum, where it merged with the Septal Prismatic Layer which was already present on the dorsum. The Septal Prismatic Layer now formed a complete lining to the body chamber and was closely connected with the insertion of septa. In small immature ribbed specimens this layer extends only one or two rib widths in front of the last septum, while in larger specimens and in the adult body chamber the front growing edge of the layer is up to $\frac{1}{8}$ whorl in front of the last septum. The position of formation of the Septal Prismatic Layer on the dorsum in small whorls before the development of ribs

could not be determined from the material available, but by analogy it was probably formed just in front of the last septum.

VIII. OCCURRENCE OF INNER SHELL

(a) *Dactylioceratidae*

The presence of an inner shell has been observed in all Dactylioceratidae that are sufficiently well preserved to show the shell structure. In the Upper Lias it is present in *Dactylioceras* (*Orthodactylites*) from the Tenuicostatum Zone (Howarth 1973), many different species of *D.* (*Dactylioceras*) from the Exaratum, Falciferum and Commune Subzones, and in the genera *Nodicoeloceras*, *Peronoceras*, *Zugodactylites*, *Porpoceras*, *Catacoeloceras* and *Collina* (Guex 1970). No well-preserved specimens have been seen that do not have an inner shell. In many examples of *Dactylioceras* (*Orthodactylites*) from the Tenuicostatum Zone of the Yorkshire coast, *Dactylioceras commune* (J. Sowerby) from the Yorkshire Commune Subzone and *Peronoceras* and *Zugodactylites* from the Northamptonshire *Leda ovum* Beds, it can be seen that the front edge of the inner shell is between $\frac{1}{8}$ and $\frac{1}{4}$ whorl behind the adult mouth border. No differences between genera and species have been detected in this respect, and in many specimens it can be seen that the front edge of the inner shell is similar in shape to the mouth border, i.e. approximately radial, but there is no rostrum on the venter. An inner shell is also developed in the Lower Liassic genus *Prodactylioceras*, for several well-preserved examples from the Davoei Zone of the Dorset coast, Gloucestershire and Oxfordshire show the hollow ribs of the main shell and the flat-topped ribs of the inner shell very well. In this genus the inner shell does not appear to extend further forwards than $\frac{1}{2}$ whorl behind the mouth border. No Middle Liassic Dactylioceratidae of the genera *Prodactylioceras* and *Reynesoceras* have been seen that are sufficiently well preserved to show the shell structure, and this is the only significant group in which the presence of an inner shell has yet to be proved.

(b) *Other ammonites*

Many other well-preserved Jurassic and Cretaceous ammonites have been examined, but an inner shell like that in the Dactylioceratidae has not yet been found in any other group. Middle and Upper Jurassic Perisphinctidae are the most likely group to have an inner shell, for some of them are homeomorphs of Dactylioceratidae, but in a number of very well-preserved examples from different horizons it can be shown that only a main shell is present. This is based on optical microscope examination, where it is seen that there are no rib cavities and that the shell is of uniform thickness, but electron microscope confirmation of the absence of an inner shell has not been made. There are, however, structures in some members of the Middle and Upper Triassic family Trachyceratidae that can only be due to the development of an inner shell like that in Dactylioceratidae. They are shown by *Maclearnoceras enode* Tozer and *Frankites sutherlandi* (McLearn), both from the Upper Ladinian of British Columbia (Tozer 1967 : 29-30, pl. 8, figs 8-12 ; 1972 : 640-641, fig. 2, pl. 128, figs 3-9). The inner shell lines the body chamber, and ends

only a short distance behind the aperture, where an abrupt transition is seen on the internal mould between the strong ornament on the inside of the main shell and the much weaker ornament on the inside of the inner shell. The inner shell is in contact with the whole of the inside surface of the main shell, so that cavities are not formed inside the ribs. *Maclearnoceras* has strong ribs on the main shell, but the inner surface of the inner shell is completely smooth. In *Frankites* the ribs are less strong and are reduced, but still present, on the inside of the inner shell. It is possible that an inner shell is a feature of many Trachyceratidae, and well-preserved aragonite material would be worthy of electron microscope investigation.

Other structures that are widely developed in Jurassic and Cretaceous ammonites, and which might be comparable with the inner shell or the Septal Prismatic Layer of Dactylioceratidae, are floors below hollow keels and spines, and dorsal shields. Hollow keels and spines cut off by floors have been frequently observed (Hölder 1952). The structure of the floors was first investigated in detail by Erben (1972), who showed that they were part of the Inner Prismatic Layer. The spine floors figured by Erben (1972: pl. 1, fig. 1; pl. 2, fig. 1; pl. 3, fig. 1) bear a close resemblance to the rib floors in Dactylioceratidae when they first appear and are formed by splitting of the Inner Prismatic Layer (Pl. 8, fig. 2). They differ, however, in having one or more chitinous membranes within that layer, which divide the prismatic layer that lines the inside of the spine from another layer added on the inside of the spine again and then also forms the flat floor below the spine. The conchiolin membranes indicate time pauses between the separate layers, and it is possible that only the outermost layer is properly called the Inner Prismatic Layer, while the layer forming the floor may be more comparable with the Septal Prismatic Layer, having been formed further back in the body chamber. Keel floors were also figured by Erben (1972: pl. 3, figs 2, 3; pl. 4) and consist of a thick prismatic layer. However, the prismatic structure of the floor is not apparent from Erben's figures, so a preparation of the same material was made and investigated. Pl. 9, fig. 6 shows the hollow keel and floor of *Eleganticeras elegantulum* (Young & Bird) from Glacial Drift, *ex* Upper Lias at Ahrensburg, Germany. It is from the end part of the phragmocone just before the body chamber, at a shell diameter of about 50 mm. The floor consists of a thick prismatic layer which is continuous with the Inner Prismatic Layer that lines the inside of the keel above the cavity. Other preparations confirm that there is no discontinuity in the prisms where the floor meets the lining inside the keel, and they also show that this is the Inner Prismatic Layer that is attached direct to the inside of the Nacreous Layer. There are considerable resemblances with the Septal Prismatic Layer in Dactylioceratidae, and it is clear that whenever features such as keels and spines are to be smoothed out before insertion of the septa, this can be done by further growth of the Inner Prismatic Layer in the rear part of the body chamber.

The term 'dorsal shield' was used by Casey (1962: 264) for a layer secreted on the dorsum of the body chamber in *Douvilleiceras* to smooth out the very large tubercles of the venter of the preceding whorl. It bears some resemblance to the dorsal development of the Septal Prismatic Layer in Dactylioceratidae, inasmuch as the layer bridges between the crests of the ribs and the tubercles leaving cavities below.

Details of the structure of the layer and its point of formation within the body chamber have yet to be investigated. Somewhat similar are the spirally ornamented dorsal layers of *Amaltheus* (Walliser 1970: pl. 4, fig. 5) and *Discotropites* (Tozer 1972: 642). They may be part of the Inner Prismatic Layer or another prismatic layer added later, but details of their structures are not known.

IX. NOMENCLATURE

The nomenclature used in this paper for the individual layers of the Dactylioceratidae shell has been given on p. 50. For the main shell it is in accordance with the general consensus of opinion of most authors who have described shell structure recently, and in particular it has been used by Birkelund & Hansen (1968, 1974), Erben, Flajs & Siehl (1969), Drushits & Khiami (1970) and Erben (1972). This nomenclature has also been used successfully for *Nautilus* and fossil nautiloids (Erben, Flajs & Siehl, 1969: 6). Terminology used by some other authors involves the adjectives 'porcellaneous' or 'spherulitic' instead of 'prismatic' for the inner and outer layers, and various uses of the terms 'ostracum' and 'hypostracum'. It is hoped that the nomenclature can now be stabilized and that the terms 'Inner Prismatic Layer' and 'Outer Prismatic Layer' will be used. There is little to be gained by use of the terms 'ostracum' or 'hypostracum' as alternatives for different divisions of the main shell, especially as they have been applied in conflicting senses by different authors (Stenzel, 1964: K77; Erben, Flajs & Siehl, 1969: 6), and their application to fossil cephalopods is not recommended. The term 'periostracum' is to be retained, however, for the organic (conchiolin) layer deposited dorsally just in front of the aperture in *Nautilus*. This is the 'black layer', and was probably present in ammonites. These are the terms that will be used in the projected revision of the Ammonoidea volume of the *Treatise on Invertebrate Paleontology*.

In view of the consistent nomenclature now used by most authors, it is unfortunate that different terms were used recently for Triassic ammonites by Tozer (1972), which will lead to confusion if perpetuated. His 'Outer Test' and 'Inner Test' were derived from Casey's (1961: 178) 'outer layer of test', proposed originally for the Outer Prismatic Layer and the Nacreous Layer, and his 'inner layer of test', proposed for the Inner Prismatic Layer which alone forms the dorsal wall of the shell in some ammonites. However, Tozer used 'Outer Test' for the Outer Prismatic Layer only, and 'Inner Test' for the Nacreous and Inner Prismatic Layers. They are unnecessary terms, for the shell layers are more exactly described by the terms Outer Prismatic, Nacreous and Inner Prismatic Layers, even when the detailed structure cannot be seen owing to recrystallization, because enough can usually be deduced by comparison to relate the shell to those layers. Tozer also referred to his 'Inner Test' as 'secondary deposits', because it was deposited after the Outer Prismatic Layer. But the Nacreous and Inner Prismatic Layers are not secondary in a diagenetic sense, and the term 'secondary deposits' is better reserved for the secondary deposits of calcite that are frequently formed inside cephalopod septal chambers during the process of fossilization.

The choice of suitable terminology for the extra layers in Dactylioceratidae presents some difficulties. Guex's (1970 : 339) term 'Preseptal Layer', which was adopted by Tozer (1972 : 640), is unfortunate now that electron microscope investigation has revealed that three new layers are added, and it is better to use terms that describe their structural appearance. Outer Prismatic Layer is used for the layer that forms the floors to the rib cavities, and Inner Nacreous Layer for the thick layer formed immediately afterwards ; these two layers form the Inner Shell, a term first used by Howarth (1973 : 250) to describe the inner of the two shells that are so clear in any well-preserved Dactylioceratidae. At a later stage the last shell layer, the Septal Prismatic Layer, is formed at the rear of the body chamber, and is so called because of its continuity with the septa. This terminology results in two Outer Prismatic Layers in the shell of Dactylioceratidae, one in the main shell, the other in the inner shell, but different terminology for the four prismatic layers leads to worse complications, especially when the structure is traced through ontogeny or compared with shells of normal ammonites. It is highly desirable to retain the normal terminology for the main shell, and then all the changes in nomenclature that occur when the Inner Prismatic Layer splits up during ontogeny are confined to those layers added on the inside that are unique to Dactylioceratidae.

X. FUNCTION OF THE INNER SHELL

The function of the inner shell can only be a matter for speculation, and Tozer (1972 : 641) has discussed some of the possibilities. It is probable that its function was similar to that performed by dorsal shields and by the septa which cut off keels and spines in other ammonites. All these structures served to eliminate or reduce the relief of morphological features that might impede movement of the ammonite. In the case of a long spine, once deposition of the main shell was complete, the ammonite would withdraw the mantle from contact with the inside of the spine, probably because a bulge of mantle and soft parts into the spine would interfere with the forward movement prior to the formation of a new septum. Instead, the mantle was stretched across the base of the liquid-filled spine, and this was sufficient to reactivate deposition of shell material at the mantle surface. By cutting off spines and keels in this way the inside of the body chamber was smoothed, so that forward movement during growth was easier and the septa could be attached to a more even surface. The complete inner shell in Dactylioceratidae seems to have been an extension of such extra shell deposition and was probably merely fortuitous to that family.

If smoothing of the inside of the body chamber was the main result of the acquisition of an inner shell, then other effects would be alteration in the strength and weight of the shell and in its attitude during life. The strength of the shell would be increased because of the box effect of the hollow ribs. The weight would also be increased, and must have been compensated for by reducing the amount of liquid in the chambers of the phragmocone. An alternative explanation is that Dactylioceratidae may have had considerably thinner main shells than other ammonites, so that the total weight of the shell was not increased, but there is no comparative

data on this point. The attitude of the shell when in buoyant equilibrium in sea-water would have been affected because inner shell is absent in the last $\frac{1}{8}$ – $\frac{1}{4}$ whorl before the aperture. This final portion would be relatively lighter than the rest of the shell in which the inner shell is complete, and the equilibrium position would then be with the aperture held higher than in a normal ammonite. This may have been somewhat disadvantageous for Dactylioceratidae if the resulting position was with the aperture pointing nearly vertically upwards.

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